

Variation in Grasshopper (Acrididae) Densities in Response to Fire Frequency and Bison Grazing in Tallgrass Prairie

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ABSTRACT While weather can contribute significantly to grasshopper population dynamics in North American grasslands, local environmental conditions resulting from land use practices may be equally important. In this study, significant differences in grasshopper density were detected among adjacent watersheds from Kansas Flint Hills tallgrass prairie that differed in fire frequency and especially bison grazing treatments. Grasshopper densities were ≈ 2.5 times greater in grazed watersheds compared with ungrazed ones. Grasshopper densities also varied somewhat in response to fire frequency, mostly in species-specific ways. No treatment interactions on overall grasshopper density were detected. The effects of fire frequency and bison grazing were implemented in part through their combined effect on the structural heterogeneity of vegetation, and other habitat characteristics. Individual grasshopper species responded uniquely to combinations of fire frequency and bison grazing. Grazing resulted in significant increases in density for seven of the nine most abundant species; fire frequency affected two species; and one species did not respond to either fire or grazing. Understanding effects of habitat on grasshopper densities provides opportunities to manage these populations for economic or conservation needs.

KEY WORDS bison grazing, Konza prairie, Orthoptera, population dynamics, prescribed burning

GRASSHOPPER ABUNDANCES IN NORTH American grasslands are highly variable (Capinera 1987, Fielding and Brusven 1990, Joern and Gaines 1990). Studies of environmental factors that underlie grasshopper population fluctuations have often focused on variable weather conditions (Dempster 1963, Capinera 1987, Johnson and Worobec 1988, Capinera and Horton 1989, Fielding and Brusven 1990). In grassland, however, weather is just one important ecosystem driver among several, including fire, grazing, or other differences in land use, that may contribute significantly to changes in grasshopper populations (Jonas et al. 2002, Fay 2003). This study examines the significance of fire frequency and bison grazing in tallgrass prairie to explain variation in habitat-specific grasshopper population densities.

Factors affecting fecundity, survival, and dispersal of individuals ultimately determine population abundance. Extrinsic environmental factors resulting from weather and land use can affect individual grasshopper performance that determines population dynamics in density-dependent ways (Pitt 1999). For example, food quality and its abundance (Simpson et al. 1995, Raubenheimer and Simpson 1997, Joern and Behmer 1998), availability of suitable microhabitat

with optimal thermal characteristics (Anderson et al. 1979, Kemp 1986, Chappell and Whitman 1990, Coxwell and Bock 1995), and likelihood of risk from natural enemies (Rothley et al. 1997, Pitt 1999, Danner and Joern 2003a, b) can each directly alter survival or reproduction by individuals and affect populations, and each can be mediated by weather. Habitat characteristics that are determined by fire and grazing can influence each of these attributes as well (Frank et al. 1998, Knapp et al. 1998a), thus affecting grasshopper population dynamics. Fire and grazing in grasslands can each lead to changes in food quality and vegetation structure that may affect susceptibility to predation, or affect opportunities for thermoregulation that is so critical to grasshopper performance. In this study, all sites experience the same weather conditions, thus permitting the importance of habitat modification from fire frequency and bison grazing and their interactions to grasshopper population densities to be assessed.

Comparisons among sites with different management treatments at watershed levels can delineate state-dependent conditions that vary along a continuum from unfavorable to ideal with respect to their influence on grasshopper abundances. Species-specific responses by grasshopper species to habitat conditions undoubtedly differ as well. Moreover, population processes that determine variation in grasshopper abundance are multifactorial (Belovsky and

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Joern 1995) such that weather combines with site-specific characteristics and individual species needs to determine abundances (Kingsolver 1989, Dunham 1993). Because fire frequency and bison grazing alter habitat characteristics important to grasshoppers (Vinton et al. 1993; Hartnett et al. 1996, 1997; Frank et al. 1998), including factors such as plant species diversity, vegetation structure, food plant quality, and litter depth, one expects them to contribute to resulting patterns of abundance.

This study examines the response of grasshopper populations to long-term application of different fire frequencies and bison grazing treatments in tallgrass prairie using experimental manipulations of whole watersheds. Two main predictions were examined. Grasshopper population densities are expected to increase in response to bison grazing because grazing can result in higher plant nutritional quality through nutrient input and elevated nutrient cycling (Frank and Evans 1997, de Mazencourt et al. 1999, Johnson and Matchett 2001, Augustine 2003, Bakker et al. 2004), and increased heterogeneity in vegetation structure (Dennis et al. 1998, Frank et al. 1998, Fuhlendorf and Engle 2001), providing more suitable habitat for thermoregulation affecting food processing rates (Yang and Joern 1994, Harrison and Fewell 1995). Fire at infrequent intervals makes plant nutrients available as transient pulses that facilitate an increase in food availability with removal of light limitation (Blair 1997, Blair et al. 1998). Such responses also potentially increase food quality to grasshoppers. Also, increased plant species richness found at sites with infrequent fires compared with annually burned and unburned sites may be conducive to increased densities of grasshoppers (Evans 1984, 1988), possibly acting to increase overall food availability to more grasshopper species. Based on these relationships, annually burned or unburned areas should support lower grasshopper densities than found at sites burned at infrequent intervals.

Materials and Methods

Grasshopper density was sampled in representative midcontinental Flint Hills tallgrass prairie at the Konza Prairie (near Manhattan, KS). Konza Prairie is a large protected research site (3,500 ha) with long-term, watershed-level burning and bison grazing experimental treatments. Samples from 33 sites including upland and lowland habitat from 20 watersheds scattered throughout the landscape were made to investigate the contribution from combinations of 4 long-term burn intervals with and without bison grazing to resulting grasshopper densities.

Konza Prairie. Fire interval and bison grazing treatments applied at the watershed level comprise the long-term management of the site. Knapp et al. (1998b, 1999) provide a detailed description of Konza Prairie and the long-term experimental plan employed at this site. Late-spring prescribed burning treatments are applied to replicate watersheds at planned intervals of 1, 2, 4, and 20 yr. Burning treatments on some

parts of Konza Prairie date to 1972, with new watersheds added as land was acquired. Bison were introduced in 1987, and the herd increased until 1992. Since 1992, the herd has been maintained at ≈ 200 individuals with unrestricted access to a 1,012-ha portion of the site, including 10 watersheds subjected to different burn frequencies of late-spring prescribed fire. On average, bison at this density remove $\approx 25\%$ of the aboveground net production annually (Knapp et al. 1999), and $\approx 90\%$ of bison diet consists of grasses (van Vuren and Bray 1983, Steuter et al. 1995). No water or supplemental food is provided to the bison herd. All watersheds include distinct topographic gradients over which both soil type and depth vary in ways that determine a variety of vegetation characteristics (Knapp et al. 1998b).

Over 500 plant species are found at Konza Prairie, $\approx 80\%$ of which are forbs; 80% of the total vegetation biomass is grass (Knapp et al. 1998a, b). Bison grazing at Konza Prairie creates a mosaic of patches of highly variable canopy structure (Bakker et al. 2003) and a redistribution of plant nutrients through deposition of dung and urine that possibly triggers various feedbacks affecting plant nutrient availability, and consequent palatability and production (Steinauer and Collins 1995, 2001).

Grasshopper Sampling. Grasshopper density was estimated at 33 sites using a standardized ring sampling technique (Onsager 1977, Onsager and Henry 1977). Samples were taken over an approximately 2-wk period in mid-August, 2002; each site was sampled once. At each site, 4 transects of 20 randomly placed rings of 0.1-m² area were used to sample grasshopper densities; transects were located 10 m apart with the first one placed arbitrarily. Rings were placed randomly and centered on the transect with the constraint that they could not be closer than 2 m from one another. Rings were left undisturbed for a minimum of 8 h before scoring grasshopper densities; ≈ 8 sites per day could be sampled in this manner if weather conditions met the criteria of sunny skies and wind speed < 15 mph. To estimate densities, I slowly walked along each transect and counted the number of grasshoppers in each ring. This technique is highly reliable and repeatable (Onsager and Henry 1977). The average density for the 4 transects at each site was used in statistical analyses. Densities of individual species at each site were determined by multiplying the proportion of each species in the grasshopper community by the overall density of grasshoppers. Relative abundances of grasshopper species were determined using sweep sampling (Evans et al. 1983). At each site, 400 sweeps were taken (combined from four 100-sweep transects), all grasshoppers identified to species, and the relative proportion of each species was determined.

Habitat Attributes. Habitat attributes were characterized along a separate 30-m transect that was established arbitrarily at each grasshopper sampling site.

To estimate grass and forb biomass (g/m²), vegetation was sampled at each site by clipping all vegetation along three 0.1 \times 3-m swaths randomly located

along a 30-m transect. Grasses and forbs were separated, dried, and weighed.

Vegetation canopy height to the nearest cm was estimated by determining the height of the vegetation using a graduated stick (mm graduations) (Wiens 1974). Twenty measurements were made along a 30-m transect. Structural heterogeneity of vegetation was estimated as the coefficient of variation (CV) of canopy height based on these measurements.

Plant species richness at each site was estimated at each site by counting the number of plant species in each of ten 0.25-m² quadrats, randomly located along the 30-m transect described above. Identities of all plant species were not established.

Bison roam freely among burn treatments throughout the grazed portion of Konza Prairie. Even areas with generally less-preferred forage are visited throughout the year at irregular and currently unpredictable schedules, including during the growing season when sites with more palatable forage exist. While bison do not graze indiscriminately across the landscape or in local areas (Knapp et al. 1999), sites located far apart in different watersheds can be considered independent of one another. Recent grazing activity at each site was classified based on an ordinal scale: 0 (nongrazed sites; no evidence of recent grazing because bison never present), 1 (no recent grazing, but site located in grazed area), 2 (small amount of grazing evident, probably by one or two animals), 3 (moderate grazing from many animals; many grazed patches interspersed in ungrazed matrix, and evidence of relatively fresh dung), 4 (extensive grazing, but grazing lawn [*sensu* (McNaughton et al. 1988)] not yet developed; evidence of large herd grazing activity, including recent dung), and 5 (extensive grazing with much return grazing leaving site characterized as a grazing lawn).

Statistical Analyses. Standard analyses (SAS/STAT, Proc GLM) based on general linear models with the method of least squares using type III sums of squares were used to evaluate primary hypotheses. Multivariate analysis of variance (MANOVA) is employed to examine treatment effects on overall grasshopper density. Fire and bison grazing treatments are crossed in a 4 × 2 factorial treatment combination over 33 sites as an unbalanced experimental design with topography nested within the fire-by-grazing treatment combinations. Fire, grazing, and topography are analyzed as fixed effects. The relative abundance for each of the species included in the analysis was >2.5% for samples from all sites combined. Overall, these nine species account for 25% of the total number of species found at Konza Prairie and ≈90% of the total abundance of individuals collected when samples from all sites are lumped. Regression analysis is also used to evaluate overall density with respect to the total number of fires since the treatments were established and the elapsed time since the last fire. A nonparametric Spearman's rank correlation (r_s) is used to evaluate the effects of recent grazing on overall grasshopper density because the data are arranged as ordinal ranks.

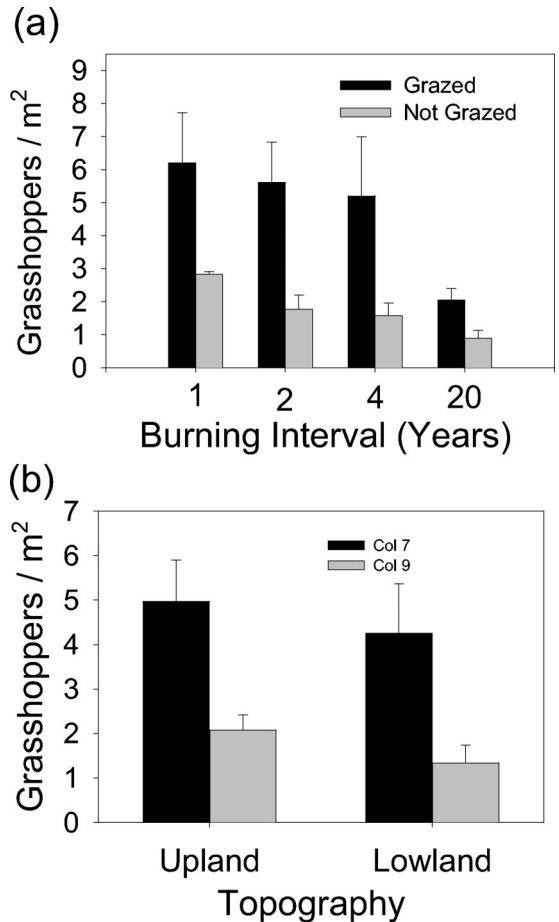


Fig. 1. Overall grasshopper density in relation to primary ecosystem drivers of fire frequency, bison grazing, and topography. (a) Effects of fire frequency and bison grazing treatments on grasshopper density. (b) Effects of topography and bison grazing on grasshopper density. Means and 1 SE are shown.

Results

A multivariate analysis shows that grasshopper density varies significantly with watershed-level effects of bison grazing (MANOVA: Wilk's λ , $F_{10,8} = 6.98$, $P = 0.006$) and fire frequency (MANOVA: Wilk's λ , $F_{30,24} = 4.12$, $P = 0.0003$) (Fig. 1a). No significant effect from a fire × grazing interaction ($P = 0.118$) or topography (Fig. 1b) nested within this interaction ($P = 0.193$) for grasshopper density was detected in the MANOVA.

Combined Grasshopper Abundances. On average, combined density for all grasshopper species is ≈250% greater in grazed areas than ungrazed areas (Fig. 1a), a significant response ($F_{1,17} = 12.2$, $P < 0.003$). Effects of fire frequency on overall grasshopper density (all species combined) were not significant ($F_{3,17} = 2.04$, $P = 0.146$) (Fig. 1a). Average grasshopper density (all species combined) in uplands compared with lowland (Fig. 1b) was not significant (topography nested fire × grazing interaction; $F_{8,17} = 0.28$, $P = 0.96$). No significant treatment interactions were observed ($P = 0.8$).

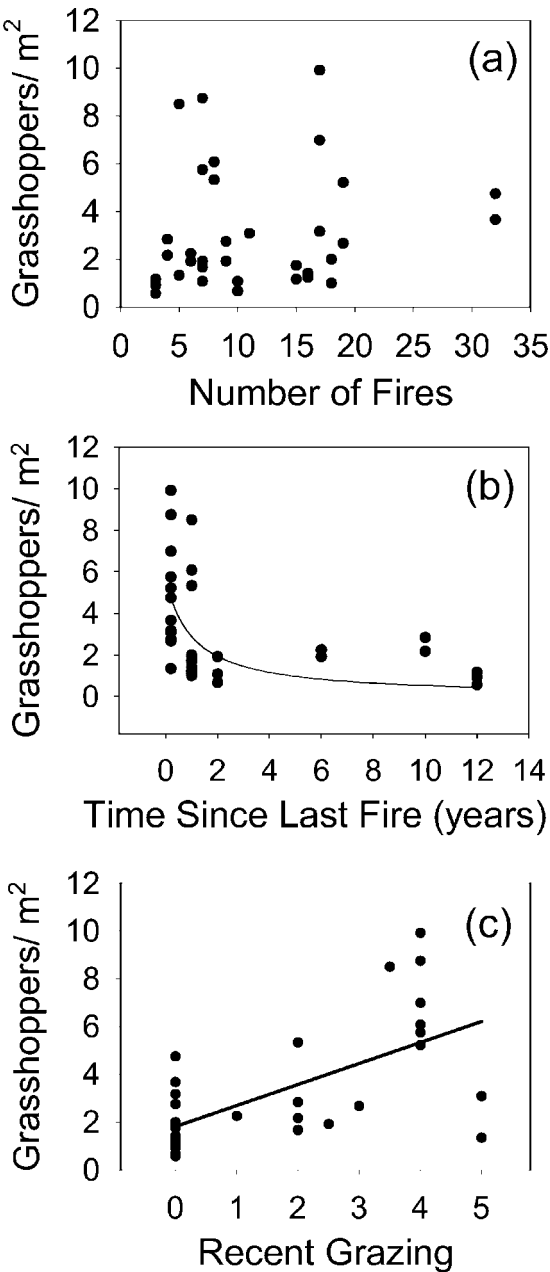


Fig. 2. Grasshopper density in relationship to: (a) number of fires over the course of the experiment (since 1972); (b) the elapsed time since the last fire, independent of overall fire frequency treatment; and (c) an ordinal classification of recent grazing impact at the site where densities were estimated (see *Materials and Methods*). Lines indicate the presence of significant relationships (see text).

The time since the last fire had a large, short-term effect on grasshopper densities (Fig. 2b) ($R^2 = 0.25$, $P < 0.001$), but the total number of fires since treatments began was not significant ($R^2 = 0.02$, $P = 0.41$) (Fig. 2a). Grasshopper abundances also increased significantly with increased levels of recent grazing ac-

tivity (Fig. 2c; Spearman rank correlation, $r_s = 0.66$, $P < 0.001$).

Influence of Habitat Characteristics. Habitat characteristics explained some of the observed variation in overall grasshopper densities among sites as seen in regression analyses (Fig. 3). In general, grasshopper densities decreased as grass biomass (lognormal relationship, $R^2 = 0.17$, $P = 0.025$) and average canopy height increased ($R^2 = 0.39$, $P < 0.0001$). Higher grasshopper densities were observed at sites with increased structural heterogeneity (CV of canopy height; $R^2 = 0.35$, $P = 0.0002$). No significant relationship was observed between overall grasshopper abundance, and forb biomass, or plant species richness.

Individual Grasshopper Species Responses to Fire and Grazing. Responses for the most abundant grasshopper species at Konza Prairie to fire and grazing are shown in Fig. 4. Density of the dominant *Phoetaliotes nebrascensis* (Thomas) was not affected by fire or grazing treatments, and density of *Hypochlora alba* (Dodge), a specialist feeder on the forb *Artemisia ludoviciana* Nutt., was only marginally affected by grazing and not by fire. Effects of bison grazing resulted in increased densities for six of nine species examined. Densities of two species were significantly influenced by fire frequency. In this study, *Orphulella speciosa* (Scudder), the second most common species, is unaffected by grazing, but reaches its highest densities in annually burned sites. Fire frequency, grazing, and a marginally significant interaction between fire and grazing were observed for *Chorthippus curtipennis* (Harris). No significant interactions between fire and grazing were detected for any of the other grasshopper species.

Discussion

Localized disturbances from bison grazing and to a lesser extent fire frequency influenced grasshopper densities in tallgrass prairie in the Kansas Flint Hills. As predicted, bison grazing activity resulted in significantly increased grasshopper densities. Contrary to predictions, infrequent fires (4-yr intervals) did not result in more grasshoppers than observed in annually burned sites, although numbers of grasshoppers dropped in relatively unburned sites (20-yr intervals). No interactions between fire and grazing were detected. Overall, grasshopper densities responded negatively to increased canopy height and total grass biomass, and positively to increased spatial variability in canopy structure; no detectable response to plant species richness and forb biomass was observed. Recent bison grazing activity and recent fire after an extended period of no burning also resulted in higher overall grasshopper densities, suggesting the capability exists for rapid responses by grasshoppers to altered habitat characteristics.

In this study, significant species-specific responses to fire frequency using density are largely absent, results that differ somewhat from those reported by Evans (1988) based on relative abundances of grasshopper species. Relative abundances of species reflect

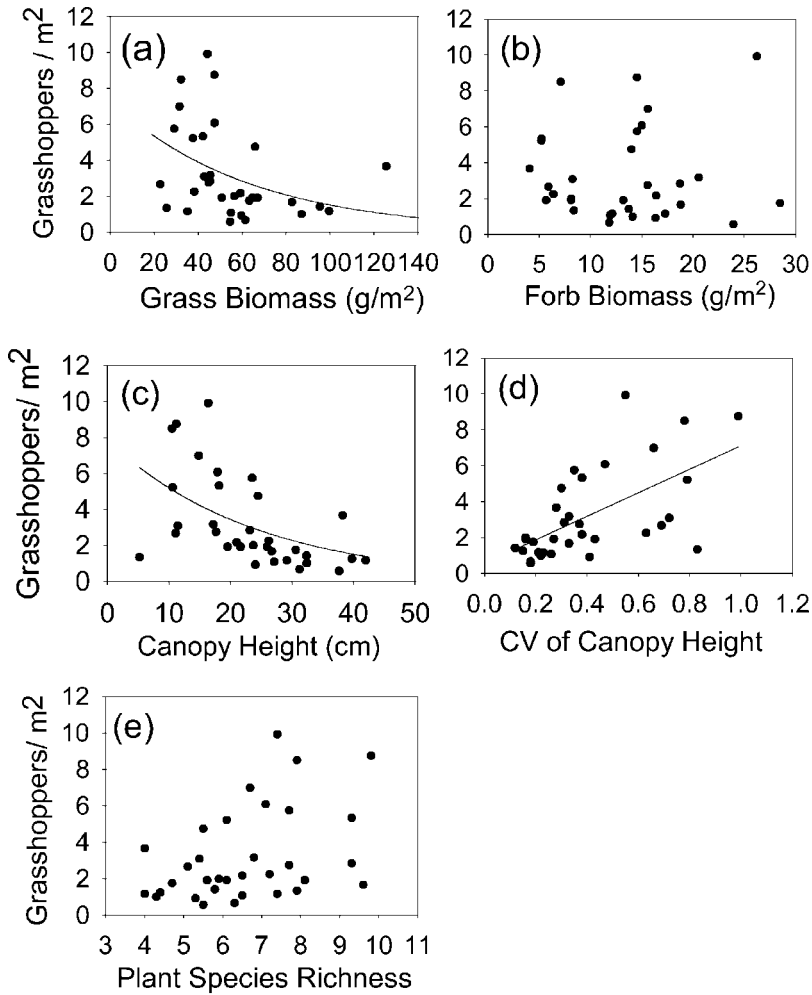


Fig. 3. Relationships between grasshopper density and habitat characteristics for all treatment combinations combined. Lines indicate the presence of significant relationships (see text).

both individual species responses as well as the overall densities of all grasshopper species (community attributes) and, thus, measure somewhat different responses than density. For individual grasshopper species, bison grazing was much more important than fire frequency for determining densities in most cases. Some exceptions were observed, including responses by the relatively common *O. speciosa*, which was much more abundant in annually burned plots independent of bison grazing activity. Also, densities of the most abundant grasshopper species, *P. nebrascensis*, were not influenced by either bison grazing or fire frequency. It remains to be seen what responses to fire and grazing might result in years when overall densities for this species are lower. An irruptive population response (Berryman 1987) to ideal weather condition, if this is the current case, may swamp out site-specific influences over the short-term.

Responses to local environmental conditions undoubtedly interact with the effects of climate to determine grasshopper abundances (Dempster 1963,

Gage and Mukerji 1977, Johnson and Worobec 1988). Weather conditions may act directly on grasshopper performance in some cases (e.g., hard freeze or weather conditions that prevent an individual's ability to regulate physiological processes). However, effects of weather on grasshopper populations are often indirect where they act by altering key features of habitats or availability of quality food, and thus influence successful survival and reproduction (Joern and Gaines 1990, Belovsky and Slade 1995, Onsager 2000). The importance of specific weather attributes to grasshopper dynamics can sometimes be dramatic, and one that varies among grassland regions, depending on overall climate characteristics (Capinera 1987, Capinera and Horton 1989), where temperature seems more important in the northern regions and precipitation in southern regions. For example, grasshopper populations from northern United States continental grasslands are influenced by temperature and generally differ from those in southern grasslands, in which precipitation plays a more important role.

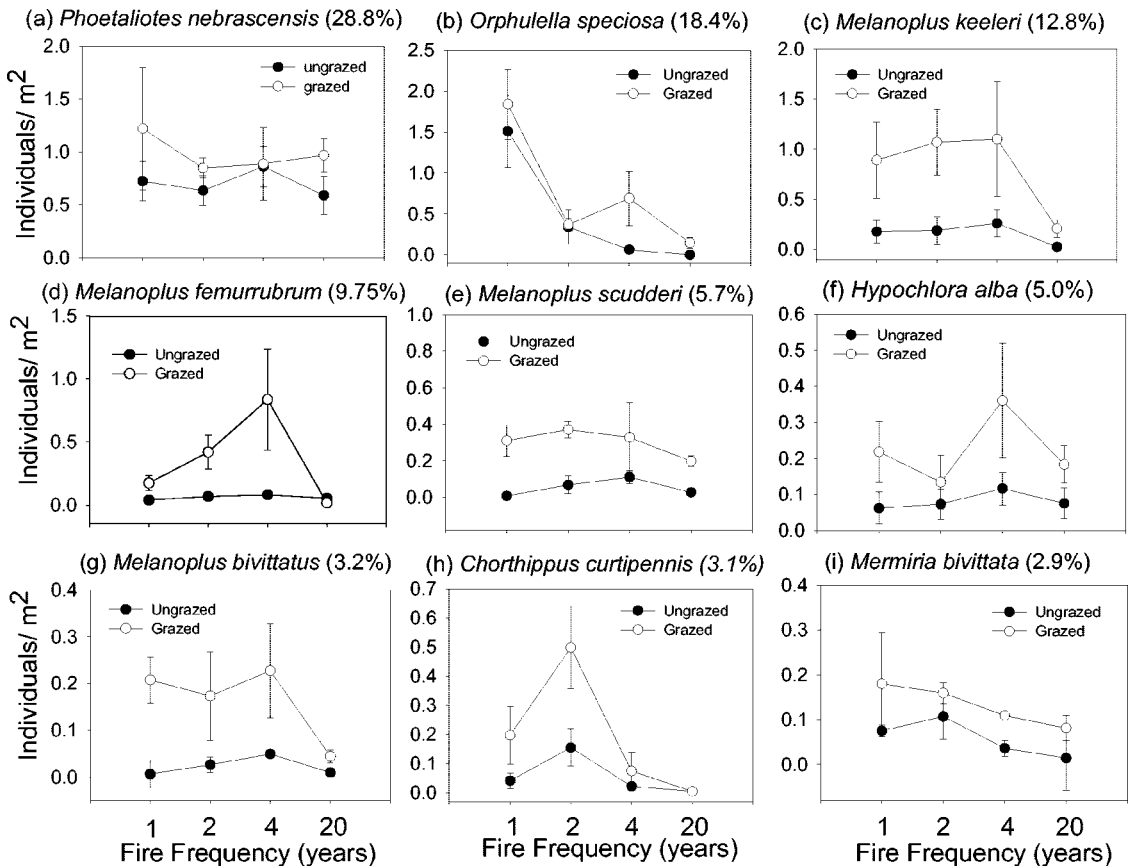


Fig. 4. Density of the nine most abundant species (a–i) at Konza Prairie in response to bison grazing and fire frequency in long-term, watershed level experiments. Overall relative abundances for each species at Konza Prairie based on samples combined from all sites are indicated in parentheses next to the species name. Means and 1 SE are shown; no significant interactions were detected. Significant treatment effects for each species include the following: (a) overall model $R^2 = 0.36$, NS both treatments; (b) overall model $R^2 = 0.67$, fire, $F_{3,17} = 9.7$, $P < 0.0006$; (c) overall model $R^2 = 0.58$, grazing, $F_{1,17} = 7.3$, $P = 0.015$; (d) overall model $R^2 = 0.65$, grazing, $F_{1,17} = 8.2$, $P = 0.01$; (e) overall model $R^2 = 0.52$, grazing, $F_{1,17} = 9.95$, $P = 0.006$; (f) overall model $R^2 = 0.35$, grazing, $F_{1,17} = 3.48$, $P = 0.07$; (g) overall model $R^2 = 0.58$, grazing, $F_{1,17} = 8.3$, $P = 0.01$; (h) overall model $R^2 = 0.77$, grazing, $F_{1,17} = 9.5$, $P = 0.007$, fire, $F_{3,17} = 9.0$, $P < 0.0009$; fire*grazing, $F_{3,17} = 2.8$, $P = 0.07$; (i) overall model $R^2 = 0.38$, grazing, $F_{1,17} = 3.66$, $P = 0.07$.

Grasshoppers can respond quickly to altered habitat condition with rapid changes in abundance. Responses to burning in this study are short-lived, lasting less than 2 yr with no obvious long-term or cumulative effect (Fig. 2, a and b). Similar responses to burning on grasshopper abundance have been observed in a variety of grassland types (Anderson et al. 1989, Bock and Bock 1991, Harper et al. 2000, Meyer et al. 2002). Grasshopper population responses to grazing can be rapid as well, as seen in the density responses to recent grazing activity (Fig. 2c) and other studies (Holmes et al. 1979, Jepson-Innes and Bock 1989, WallisDeVries et al. 1998, Onsager 2000, Jonas et al. 2002, Fay 2003). In short grass steppe with generally low plant production, however, grasshopper densities increased on relatively ungrazed pastures compared with grazed sites (Capinera and Sechrist 1982), contrary to results reported in this work. Because of the large scale at which the treatments are applied in this study, effects of fire

and grazing at the watershed scale most likely reflect demographic responses rather than movement into the sites. Responses to significant recent grazing activity (Fig. 2c) at more local scales most likely reflect a combination of demographic responses combined with short distance dispersal (Heidorn and Joern 1987) because of the smaller areas affected.

Bison grazing modifies habitats in ways that can affect grasshopper populations in a variety of indirect ways (Kemp et al. 1990, Onsager 2000). It is unlikely that bison grazing affects grasshoppers directly because of feeding or movement activities. Several underlying mechanisms that could explain the observed density responses consistent with the large-scale treatments reported in this work can be hypothesized. Food quality to grasshoppers probably increases in response to moderate bison grazing (Frank et al. 1998, Johnson and Matchett 2001) or fire (Blair 1997), reflecting tissue regrowth after leaf loss or stress induced

by trampling. Canopy density (grass biomass and canopy height) and spatial heterogeneity in vegetation structure were also correlated with grasshopper abundances at Konza Prairie. Habitat structure affects grasshopper performance in important ways by influencing escape space (the ability of individuals to avoid and actively escape from predators and parasitoids) (Dennis et al. 1998, Gratton and Welter 1999), and the ability to regulate body temperature (Gillis 1983, Willott 1997) and maintain water balance (Anderson et al. 1979). Both predation risk and thermoregulation can have great influences on individual grasshopper fitness (Yang and Joern 1994, Pitt 1999, Danner and Joern 2003b, 2004), thus affecting population dynamics. Thermoregulation, for example, is a critical activity that affects food processing and nutrient acquisition rates (Yang and Joern 1994, Harrison and Fewell 1995), or the ability to fend off pathogens with "behavioral fever" (Carruthers et al. 1992). Interactions among these mechanisms can ultimately affect grasshopper population densities, interacting with the state of the system set by current weather conditions (Begon 1983, Willott and Hassall 1998) to yield the differences among treatment combinations observed in this study.

These results extend studies of grasshopper responses to fire frequency at Konza Prairie that emphasized relative abundances of species (Evans 1984, 1988) and shift the focus to combining effects of fire and grazing, as well as examining absolute density rather than relative abundances. Some patterns of grasshopper response to fire frequency based on relative abundances remain, and others disappear when examined in terms of absolute density. For example, *O. speciosa* is most abundant in annually burned sites in both studies when considered either way. However, fire frequency did not result in significant responses for seven of the nine species that constituted 90% of the individuals in density samples collected here. There is no doubt, however, that the species composition of grasshopper assemblages varies in response to fire (Evans 1984, 1988; Joern 2005), even if fire has a smaller role to play in terms of density.

Implications for Managing Grasshopper Populations. Many factors influence the dynamics of insect populations. Increased attention is now placed on combining the influences of weather to other feedbacks intrinsic to insect-environment systems, including biotic feedbacks and attributes of habitats that influence individual performance. It is important to evaluate habitat suitability as a variable of equal standing to weather, especially because human impacts and altered land use practices can greatly influence these responses (Jonas et al. 2002). Current results illustrate their potential importance. For all practical purposes, weather acts as a largely unpredictable forcing function with respect to understanding grasshopper population dynamics, a factor that hinders forecasting activities and provides few options for its direct incorporation when developing management plans. Land use and habitat conditions are becoming increasingly recognized as important for understanding grass-

hopper population dynamics (Capinera and Sechrist 1982, Onsager 2000, Jonas et al. 2002, Fay 2003), providing opportunities to develop creative approaches to manage their densities. As indicated above, modification of habitat structure and conditions through the knowledgeable use of key ecosystem drivers such as prescribed burning and grazing can have major effects on grasshopper densities.

Controlled burning and grazing become useful tools to manipulate the system for managing populations. Range managers may be able to develop additional, feasible options to manipulate grazing to provide sustainable management of grasshopper control without relying on extensive chemical control (Onsager 2000), although much remains to study before this can be realized. While outcomes will certainly vary among grassland types, twice over grazing that leaves vegetation structure during critical nymphal periods limits outbreaks in North Dakota mixed grass rangeland (Onsager 2000). Conservation biologists charged with preserving biodiversity in grassland may be able to manage sites based on local conditions so that grasshopper densities vary in concert with natural processes, within acceptable limits to range managers while conserving local grasshopper species diversity (Joern 2005) or facilitating nutrient cycling (Belovsky and Slade 2000, Hunter 2001). In each of these goals, it is necessary to uncover mechanistic explanations for the relative roles that fire, grazing, and weather contribute to grasshopper population dynamics so that they can be managed through optimized land use practices. A model for grazing management of grasshopper populations that includes the elements described above as primary constituents is outlined in Onsager (2000), but see Capinera and Sechrist (1982) for shortgrass steppe. Such differences emphasize the need to better understand mechanistic impacts of key ecosystem drivers from multiple grasslands to devise new, sound management opportunities.

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